"Notes on the Statolith Theory of Geotropism. I. Experiments on the Effects of Centrifugal Force. II. The Behaviour of Tertiary Roots." By FRANCIS DARWIN, F.R.S., and D. F. M. PERTZ. Received May 30,—Read June 9, 1904.

I.

According to the statolith theory,* there are in plants certain cells specialised to act as organs of orientation in space; organs, in fact, functioning like the otocysts of certain animals. In both cases the sense of verticality is believed to be the result of the pressure of certain heavy bodies (usually starch grains in the case of plants), on a sensitive surface, namely, the lining membrane of the otocyst in the case of animals, or in the case of plants the protoplasm lining the statolith-containing cells (statocytes).

In a paper† dealing with the arguments for and against the theory, Jost brings forward as the most serious objection the behaviour of plants to centrifugal force. He found that plants, subjected to centrifugal force equal to from 0·02—0·05 g.,‡ exhibited curvature, but that the starch-grains were uniformly distributed throughout the statocytes, not, as should be the case according to our theory, resting on the cell walls furthest removed from the axis of rotation. Jost sees in these results an absolute proof that, in the cases investigated by him, the starch grains do not function as statoliths.

It seemed to us that this conclusion was a somewhat hasty one and we determined no longer to delay the investigation of Knight's experiment in relation to starch grains, which we had previously recognised as a necessary part of the statolith question. Our experiments were carried out on seedlings of *Setaria* and *Sorghum*, in which the statoliths are in the cells of the cotyledon (coleoptile), and in which the position of the movable starch can easily and rapidly be determined by splitting the cotyledon longitudinally and examining the two halves mounted in iodine solution. The experiments were directed to two points, viz., the centrifugal force needed to produce (*a*) geotropic curvature, (*b*) movement of starch-grains. It will be seen that our results are directly opposed to those of Jost, inasmuch as, according to us, the lowest effective centrifugal force is about the same in the two sets of experiments. The centrifugal apparatus was driven by a hot-air engine regulated by one of Griffiths's gas-regulators

* Noll, 'Heterogene Induction,' Leipzig, 1892; Haberlandt and Němec, 'Ber. Deutschen Bot. Gesellsch.,' 1900.

† "Die Perception des Schwerereizes in der Pflanze," 'Biolog. Centralblatt,' vol. 22, March 1902, p. 161.

‡ g. being the acceleration of gravity.

made by the Scientific Instrument Co. In the experiments on curvature the seedlings were cut and fixed by melted cocoa-butter to cork supports in small metal boxes, in which the air was kept damp. They were either placed tangentially at right angles to the axis of rotation, or else parallel to the axis. In the experiments on the distribution of the starch the seedlings were cut and placed in grooves in a sheet of cork, being kept in place by damp filter-paper and a second sheet of cork firmly fixed. In the majority of experiments the tip of the seedling was also fixed to a little bar of wax. The seedlings were fixed radially, the apices of some being inward and of others outward. This arrangement gives a striking result in successful experiments, for the starch travels to the apical end of the cells in the specimens whose apices point outwards, while it remains basal in the others.

(*a*) *Experiments on Curvature.*

We give our results in the form of a summary instead of publishing the details of each experiment. It will be seen that there was a good deal of irregular nutation; this is a drawback to the use of *Sorghum* and *Setaria*, but these plants being otherwise convenient we continued to employ them.

Adding together the results obtained with centrifugal forces of 0·02 g., 0·03 g. and 0·04 g. we find that

85 seedlings (68 per cent.) curved to the centre (apogeotropically).
18 „ (14·4 per cent.) did not curve at all.
22 „ (17·6 per cent.) curved away from the centre (prosgeotropically).

We conclude from these results that seedlings of *Sorghum* and *Setaria* are to some extent stimulated geotropically by a centrifugal force of from 0·02—0·04 g. The average amount of apogeotropic curvature to the centre is only 20°, and as this is the result of about 22 hours stimulation, we are justified in believing that under our conditions a definite geotropic curvature cannot with any certainty be produced with centrifugal forces of much less value than 0·02 g. The fact that observers working with different plants and by other methods have found curvature with considerably weaker centrifugal force, does not concern us, since our investigation is a comparative one.

(*b*) *The Behaviour of the Statoliths to Centrifugal Force. Horizontal Axis.*

In the first series the seedlings were all placed radially with the apex outwards for 22—24 hours. The behaviour of the starch is not uniform in the cells of the cotyledons, so that it is only possible to give a general impression of the results.

Thus "scattered and apical" means that the starch is to a great extent diffused through the cells, but that in a good many cases the starch has accumulated at the apical ends of the cells. On the other hand "apical and scattered" means that the starch is apical rather than scattered.

Table I.

Plant.	Centrifugal force.	Temperature.	Position of starch.
	g.	° C.	
Setaria.	0·02	14	Scattered and apical.
,, ...	0·02	16	Scattered, apical, and some basal.
,, ...	0·02	17	Scattered.
,, ...	0·02	17	Scattered, some apical, also some basal.
,, ...	0·02	20	Apical and scattered.

The general conclusion to be drawn is that with 0·02 g. there is a tendency, though a very slight one, for the starch to move radially and accumulate in the apices of the cells.

In Table II, the seedlings were placed both apex outwards and apex inwards; the period of exposure was about 22 hours.

Table II.

Plant.	Centrifugal force.	Temp.	Apex.	Starch.
	g.	° C.		
Setaria.	0·03	22·0	Out	Two specimens, basal and scattered; one specimen, many cells apical.
			In	Scattered and basal.
,, ...	0·03	18·5	Out	Scattered and apical.
			In	Scattered and basal.
,, ...	0·04	13—18	Out In	No distinct difference.
Sorghum and Setaria	0·04 (about)	16—20	Out	More apical than basal.
			In	Scattered and basal.
Setaria.	0·04	18—21	Out	Apical and scattered.
			In	Basal and scattered.
,, ...	0·05	21·0	Out	Scattered, many cells apical, but basal in parts.
			In	Much scattered. (Not very distinct difference between "out" and "in.")

Thus out of six experiments there was only one in which there was no difference between the starch in the seedlings pointing outwards and in-

wards. In one (0·05 g.) the difference was not distinct, while in the other four experiments the difference was distinct. This proves that the starch moves under the influence of a centrifugal force of from 0·03—0·04 g. From the prevalence in our notes of such phrases as "scattered and apical," "scattered and basal," it is evident that with 0·03 and 0·04 g. the starch does not move easily, and this is precisely what we should have expected from the small amount of curvature produced with centrifugal forces of about this magnitude.

Centrifugal Machine with Vertical Axis.—We made some use of a centrifugal apparatus with a vertical axis, in the belief that the results would be more easily observed than in the case of a horizontal axis. Supposing that the seedlings are fixed radially on the horizontal disc of the machine, the starch grains will, if the wheel is at rest, be "lateral," *i.e.*, will lie on the longitudinal cell walls which are now horizontal. When the wheel is set in motion there will be no tendency to general diffusion of the statoliths, which will remain "lateral" but will tend to accumulate at the outward extremities of the cells; the starch will be what we call "apically cornered" or "basally cornered," according as the apices or bases of the seedlings are outwards.

With regard to curvature, if the seedlings are placed horizontally and tangentially, they will of course curve upwards in response to the force of gravity, and at the same time inwards in response to centrifugal force. In a similar way, if the seedlings are placed vertically they will not grow straight upwards as they would if gravity alone was in question, but again slightly towards the centre. In those experiments in which the centrifugal force varied between 0·02 and 0·04 g., only 48 per cent. of the seedlings curved to the centre, and the average curvature was only 10°. This, perhaps, was to be expected when the centrifugal force was no more than from 2—4 per cent. of gravity.

The effect on the starch grains is shown in Table III.

Table III.

Plant.	Centrifugal force.	Temp.	Apex of seedling.	Position of starch.
	g.	°C.		
Setaria.......	0·02	18	Out	Scattered, apical-cornered, and some basal-cornered.
Sorghum.....	0·02	19	,,	Lateral and apical-cornered; some basal-cornered.
Setaria.......	0·03	16—18	,,	Lateral; some basal and apical-cornered.

On the whole, with 0·02 and 0·03 g. the movement is irregular and

slight. But the existence of a considerable number of apically-cornered cells can, we think, only be accounted for as the result of centrifugal force. Without centrifugal force the starch should have been lateral or basally cornered.

In the remaining experiments (Table IV) two sets of seedlings were used one with the apices radially outwards, the other radially inward. Here the result was more decided.

Table IV.

Plant.	Centrifugal force.	Temp.	Apex of seedling.	Position of starch.
	g.	° C.		
Setaria and Sorghum	0·03	18	Out In	Scattered and lateral; a few apical in both.
Setaria......	0·03	16	Out	Apically cornered and scattered.
			In	Basal.
,, ...	0·04	20	Out	Apical and lateral.
			In	Basal.
,, ...	0·06	20	Out	Apical, lateral; some basal.
			In	Basal, scattered.
Sorghum	0·07	17·5—20	Out	Scattered, apical.
			In	Basal.

It is clear from these results that a force of 0·03—0·04 g. has a distinct effect on the position of the starch grains. The effect of 0·06 and 0·07 g. was not materially greater than that of 0·04, and we are inclined to think that this is also true in the experiments with a horizontal axis of rotation.

Inclined Plane.—We made a few experiments, in which seedlings were fixed on plane surfaces inclined at angles varying from 2—5°. If the plane be inclined at an angle θ, the component of gravity acting in the line of the plane will be $\sin\theta$ g. Thus, if the seedlings be placed apex downwards, on a plane inclined at 2°, there will be a force equal to 0·035 g., tending to move the starch grains to the apices of the cells. Our experiments were not very numerous, but, as far as they go, they confirm the above results. We find that the statoliths are displaced by 0·035 g., but not by 0·017 g.

The Behaviour of the Statoliths on the Klinostat.—When a plant is kept slowly rotating on a horizontal axis, the practical result is that it does not bend geotropically. The result has been explained by the supposition that the plant never remains in one position long enough for the perception of gravity. But there are experiments which show that (at any rate, in certain cases) the gravitational stimulus is continuously perceived, but fails to produce a curvature, because of its

symmetrical distribution.* Our experiments tend to confirm this point of view, since they show that the statoliths are not evenly dispersed through the cells,† but that they take up more or less definite positions in different parts of the rotation. The experimental plants were, as before, seedlings of *Setaria* and *Sorghum*, cemented into boxes, or fixed between cork and damp blotting-paper, and so arranged that the axis of the plants were at right angles to the axis of rotation. The klinostat, which made one revolution in 17, 20, or 30 minutes, was placed in a dark room, where the temperature varied from 17 to 24° C. The number of seedlings used in each experiment was four, six, or eight, and, in all cases, half the number pointed in one direction, and the others in the opposite direction. Thus, at the moment at which the seedlings are vertical, half of them are "apex upward," the rest being apex downwards. The method was to leave them rotating on the klinostat, and to remove them the moment they reach the vertical, when the starch in the two lots (up and down) was rapidly compared. With a rotation of once in 30 minutes, the apex-upward seedlings will have been for $7\frac{1}{2}$ minutes passing from the horizontal to the vertical. With the 17 and 20 minute klinostats, the periods will be respectively $4\frac{1}{4}$ and 5 minutes. It will be seen in Table V that, in the first three experiments in which the duration of the rotation was short, no definite result was obtained; and the same absence of difference in the starch was noted in two other experiments in which the plants were examined, after two rotations of 17 minutes. In the remaining experiments a distinct result was obtained.

In a few experiments given in Table VI, the klinostat was stopped when the seedlings were horizontal. In this case half the seedlings ("apex last down") had for $4\frac{1}{4}$ minutes been changing from apex vertically down to horizontal, while the other lot ("apex last up") had changed from apex up to horizontal. These experiments, taken with those in Table V, show that a complete reversal of the starch from the apical to the basal ends of the cells may take place on the klinostat in $8\frac{1}{2}$ minutes.

Table VI also gives the results of three experiments, in which the seedlings were parallel to the axis of rotation, in two of which the starch was, as was expected, on the longitudinal cell walls ("lateral").

On the whole, the results of Tables V and VI show that there is no inconsistency between the statolith theory and the view above referred to, that continuous gravitational stimulation occurs on the klinostat.

The question whether $8\frac{1}{2}$ minutes, the period during which gravi-

* See Elfving 'Öfversigt af Finska Vetenskaps Förhandlingar,' 1884, and F. Darwin on "Cucurbitous Seedlings," 'Practical Physiology of Plants,' 1st edition, 1894, p. 176.

† As Jost, *loc. cit.*, p. 176, seems to believe to be the case.

Table V.—Change and Position of Starch produced by Rotation on a Klinostat.

Period of rotation of klinostat...... Expt. 1—6, 30 mins.
" " " " 7, 20 "
" " " " 8—10, 17 "

No.	Date.	Plant.	Position when stopped.	Time on klinostat.	Temp.	Seedlings, apex up, position of starch.	Seedlings apex down, position of starch.
	1901.			h. m.			
1	December 12	Sorghum	Vert. up and down	1 20	17°	Scattered	Scattered.
2	" 16	"	"	0 45	17	Basal	Basal; scattered.
	1902.						
3	January 9	Setaria	"	1 50	..	Scattered	Scattered; perhaps more apical.
4	" 10	"	"	2 20	20	Scattered; some cells basal	Scattered; some cells apical.
5	" 13	Sorghum	"	1 5	21	Scattered; many basal	Scattered; many apical.
6	" 14	"	"	19 15	..	On the whole basal	Many cells apical and apically cornered.
7	" 18	"	"	2 0	..	Basal and basally cornered; scattered	Apically cornered and scattered.
8	November 18	Setaria	"	21 41	17	Basal, basal-cornered; scattered	Scattered and apical and apically cornered.
9	" 19	"	"	21 20	20	Scattered; basal and lateral	Scattered; many apical and lateral.
10	" 20	"	"	22 11	16	Scattered; basal and lateral	Scattered; some apical.

Table VI.—Klinostat Experiments.

One rotation in 17 minutes.

Nos. 11—15, seedlings at right angles to axis of rotation, examined when horizontal.
„ 16—18, „ parallel to axis of rotation.

No.	Date.	Plant.	Position when stopped.	Time on klinostat.	Temp.	Starch, apex last up.	Starch, apex last down.
	1902.			h. m.			
11	November 21	Setaria	Horizontal	23 22	17°·5	Basal and scattered	Scattered, basal and apical.
12	„ 24	„	„	22 45	22·0	Lateral and basal	Lateral; apical and basally cornered.
14	„ 25	„	„	22 39	22·0	?	Scattered and apical.
15	„ 26	„	„	22 55	24·0	Basal and basally cornered and scattered	Apically cornered; apical and scattered.
			Seedlings parallel to axis of Klinostat.				
16	November 28	Setaria	..	24 10	20·0	Scattered and lateral	—
17	December 1	„	..	24 20	18·5	Scattered	—
18	„ 2	„	..	22 25	..	Scattered and lateral	—

tational stimulus remains unchanged in direction (though not in intensity) is long enough to be effective in producing curvature, does not concern us, since it is a question which is applicable to all theories of gravitational sensibility.

II.

On the Presence of Statoliths in Tertiary Roots.

Early in our work we noticed the existence of movable starch in the tertiary roots of *Vicia faba*, and since tertiary roots have been hitherto believed to be devoid of gravitational sensitiveness, we saw that here was a question for investigation. In Jost's above quoted paper (p. 173) this difficulty is referred to in the following words:—

"Further anatomical investigation is also needed in the case of roots. My own work has shown us that lateral roots of secondary or tertiary rank, which are not gravitationally sensitive, have just the same movable starch as primary roots."

We do not know to what secondary roots Jost refers. In the case of *Vicia faba* there is no difficulty in finding a function for the statoliths of the secondary roots, since these are well known to react to gravity. In regard to the tertiary roots the difficulty is a real one.

It is well known that, if the primary root is cut off, one or more of the secondary roots ceases to grow diageotropically, and turns vertically downward. It occurred to us that the tertiary roots springing from such a secondary might acquire gravitational sensitiveness, and behave like normal secondaries. This proves to be the case, and in this fact undoubtedly lies the explanation of the presence of statoliths in tertiary roots.

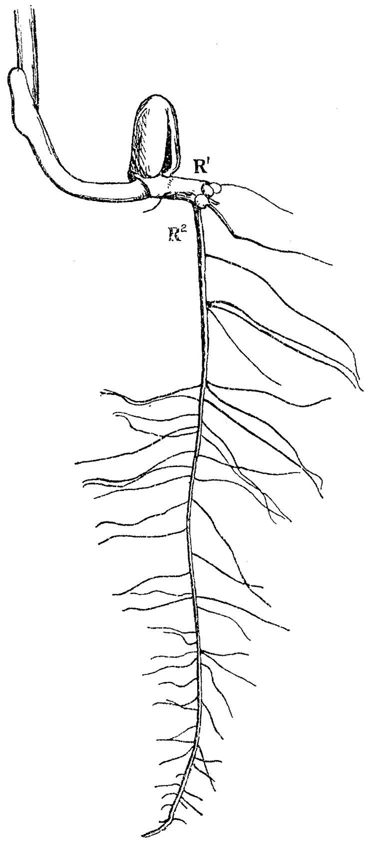
Our method of procedure is to wait until the secondary roots of a bean (*Vicia faba*) have begun to show themselves, when the primary root is cut near its base, and the secondary roots, with the exception of one, are at the same time removed. The seedling is then planted with the stump of the primary root roughly horizontal, and the single secondary root pointing vertically downwards, as shown in fig. 1. It will be seen that the secondary root R^2 grows vertically for the greater part of its length, and that the general direction of growth of the tertiary roots is strikingly like that of normal secondaries; and this preparation alone would strongly suggest, to anyone accustomed to the subject, that under these conditions the tertiaries were regulated by gravitation.

We grow our bean roots (in a dark room) in Sachs's troughs, having oblique glass sides, so that the secondary root, in its attempt to grow vertically, is forced to follow the glass wall. This insures that the secondary root, and a fair proportion of tertiaries, shall be visible, and thus their course can be recorded by painting lines on the glass.

Care is necessary, at the beginning of the experiment, to prevent more than one secondary root developing; the primary root should at first be uncovered every day, and any young secondaries pinched off.

The preliminary arrangement takes some time; thus, for instance, a primary root was amputated February 6, and the tertiary roots were not ready for observation until February 16.

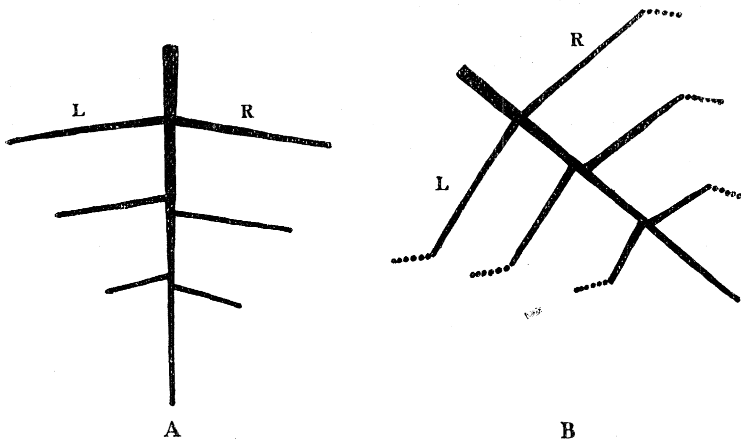
Fig. 1.



The method was that of Sachs, which may be illustrated by the following diagram (p. 487).

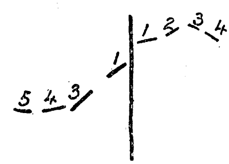
Fig. 2, A shows a primary root growing vertically, and giving off, to the left and right, two sets of secondaries, L and R, which have assumed their usual lines of growth somewhat below the horizontal. The trough is now raised at one end, as in fig. B; the roots L and R are affected in opposite ways by this change, the L roots are now 45° below, while the R's are 45° above their normal line of growth, the consequence is that the L's bend up and the R's down, as shown by the

FIG. 2.



dotted lines in fig. B. Fig. 3 shows the similar behaviour of tertiary roots.

FIG. 3.



The line representing the secondary root is vertical and unbroken, the curved lines springing from it on the left and right are tertiaries, and are made up of separate sections, each of which represent the growth on one day. The marks 1 and 1 were painted on May 12, 1903. They show that the R and L roots grew out at very different angles with the secondary root. This is accounted for by the fact that while sections 1 and 1 were developing the left end of the trough was raised (25°). If the figure is turned to this position it will be seen that 1 and 1 make roughly equal angles with the horizon.

After tracing sections 1 and 1 the trough was raised so as to make 40° with the horizon, the left end being still the higher.

On May 13, section 2 was painted on the R side, section 2 on the L side could not be clearly seen. The trough was now placed at an angle of 32°, being, however, reversed, so that the R end was higher.

May 14, sections 3 painted on both sides. It will be seen that root R has begun to assume its proper angle below the horizon, whereas L has continued to grow nearly in line with section 1. On the following days (sections 4 and 5) L bent upwards. This is a striking

instance of what we have observed in other cases, viz., that tertiary roots bend downwards more readily than upwards. It is interesting because it is a point of resemblance between them and diageotropic secondary roots. The slowness of the growth of the tertiaries in this experiment was probably due to the development of more than one secondary root.

FIG. 4.

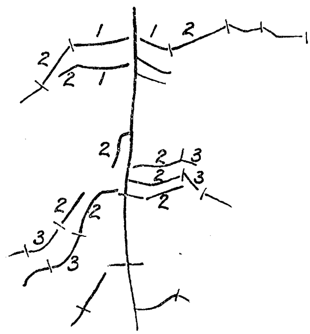


Fig. 4 shows the same state of things, namely, that the direction of growth of the sections marked 2 is different on the two sides. Thus section 2 is directed obliquely upwards in the right-hand tertiary roots, and downwards on the left. A similar contrast exists between the sections marked 3. These changes of direction are due, as in fig. 3, to changes in the position of the trough.

In the later experiments, of which fig. 5 is an example, the tracings were made each day in a different coloured paint, so that a complete record of all tertiaries was obtained. This was not the case in fig. 4, so that some of the sections are necessarily left without numbers.

In fig. 5, the numbers 1, 2, 3, etc., give the tracings made on successive days. It will be seen that in the younger part of the root, near the lower end of the figure, the sections of the tertiary roots do not begin with the numerals 1 or 2, but with 5, 6, or 7; this is because when sections 1 and 2 were traced, the lower (younger) tertiaries had not yet appeared.

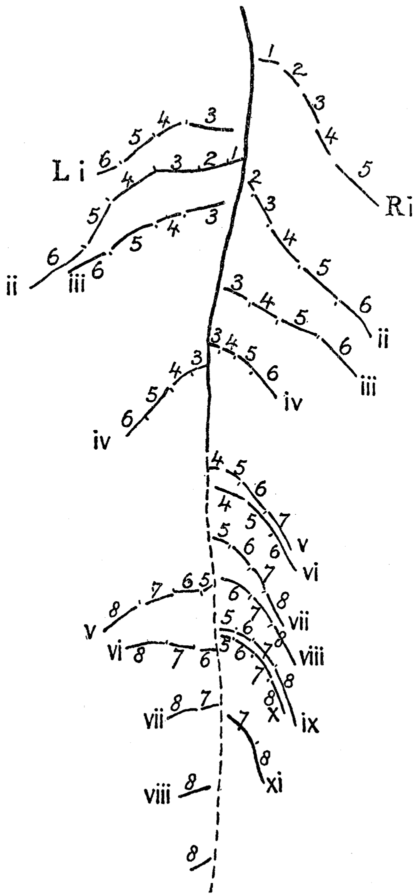
After section 1 was traced, the trough was tipped up at an angle of 39° (right side highest), and remained in that position while 2 and 3 developed. This accounts for the bend downwards in the oldest root on the right (R i), and the slight upward bend in L ii (section 3).

The trough was now reversed, being placed at 19° (left side highest) and being allowed to remain in that position while sections 4 and 5 developed. It will be seen that the curvature of the sections 3, 4, 5 is upward on the right (except in root R iv) and downwards on the left.

The trough was again reversed after a tracing of 5 had been made, the right side being now higher, and the angle about 30°. Here again the roots on the right bend down and on the left up, as will be seen by comparing sections 5 and 6.

The roots, therefore, show clearly a power of curving up or down so

Fig. 5.



as to assume their proper angle with the horizontal just as normal secondary roots do in similar circumstances. The only obvious exceptions to the rule are in roots R iv, v, vi, where a downward bend occurs between sections 3 and 5 or 4 and 5, as the case may be; here the curve should either have been absent or in the upward direction.

After section 6 was traced the trough was exposed to light and sections 7 and 8 were traced. It will be seen by comparing 6 and 8,

that in both sets of tertiaries (right and left) there is a tendency to curve downward—and this is well known to occur in normal secondary roots exposed to light, and is another instance of the assumption by the tertiaries of characters hitherto associated only with secondary roots.

The facts above given prove that when the primary root is removed and a secondary root assumes its place, the tertiary roots take on the character of normal secondaries. It may be believed, therefore, that the existence of statoliths in normal tertiary roots is a provision enabling them to assume diageotropic growth in case of injury to the primary root. This, though appearing a bold conclusion, does not involve an adaptive action different in principle from the well-known assumption by secondary roots of the characters of the primary root.

We desire to express our thanks to Mr. T. Elborn, Assistant in the Cambridge Botanical Laboratory, for the help he has given us during the course of our research.

"On the Electric Effect of Rotating a Dielectric in a Magnetic Field." By HAROLD A. WILSON, M.A., D.Sc., Fellow of Trinity College, Cambridge. Communicated by Professor J. J. THOMSON, F.R.S. Received May 18,—Read June 2, 1904.

(Abstract.)

It was shown by Faraday in 1831 that an electromotive force is induced in a conductor when it moves in a magnetic field so as to cut the lines of force. The object of the experiments described in this paper was to see if a similar electromotive force is induced in a dielectric when it moves in a magnetic field.

According to Maxwell's electromagnetic theory, as developed by H. A. Lorentz and Larmor, such an electromotive force should be induced in a dielectric, and should be equal to that in a conductor multiplied by the factor $1 - K^{-1}$, where K is the specific inductive capacity of the dielectric.

The method employed was to rotate a hollow cylinder of ebonite in a magnetic field parallel to the axis of the cylinder. The inside and outside surfaces of the cylinder were provided with metal coatings with which electrical contact was made by sliding brushes. The inside coating was connected to earth, and the outside coating to one pair of the quadrants of a sensitive quadrant electrometer, the other pair of quadrants being connected to earth. The magnetic field was then reversed, so reversing the induced electromotive force in the ebonite. The resulting electric displacement was measured by means of the